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Dyadic visual perceptual learning on orientation discrimination

Highlights

- Dyadic VPL leads to greater behavioral improvement and a faster learning rate
- Performance difference between partners modulates the facilitating effects
- Dyadic VPL augments orientation representation refinement in the visual cortex
- Dyadic VPL strengthens connectivities between social and visual cortical areas

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In brief

Zhang et al. reveal that learning with a partner can facilitate visual perceptual learning (VPL), leading to greater behavioral improvement and a faster learning rate. The neural mechanisms involve refined visual representations and enhanced connectivities between social and visual cortical areas.

Zhang et al., 2023, Current Biology *33*, 2407–2416
June 19, 2023
https://doi.org/10.1016/j.cub.2023.04.070

CellPress

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Dyadic visual perceptual learning on orientation discrimination

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https://doi.org/10.1016/j.cub.2023.04.070

SUMMARY

The belief that learning can be modulated by social context is mainly supported by high-level value-based learning studies. However, whether social context can even modulate low-level learning such as visual perceptual learning (VPL) is still unknown. Unlike traditional VPL studies in which participants were trained singly, here, we developed a novel dyadic VPL paradigm in which paired participants were trained with the same orientation discrimination task and could monitor each other's performance. We found that the social context (i.e., dyadic training) led to a greater behavioral performance improvement and a faster learning rate compared with the single training. Interestingly, the facilitating effects could be modulated by the performance difference between paired participants. Functional magnetic resonance imaging (fMRI) results showed that, compared with the single training, social cognition areas including bilateral parietal cortex and dorsolateral prefrontal cortex displayed a different activity pattern and enhanced functional connectivities to early visual cortex (EVC) during the dyadic training. Furthermore, the dyadic training resulted in more refined orientation representation in primary visual cortex (V1), which was closely associated with the greater behavioral performance improvement. Taken together, we demonstrate that the social context, learning with a partner, can remarkably augment the plasticity of low-level visual information process by means of reshaping the neural activities in EVC and social cognition areas, as well as their functional interplays.

INTRODUCTION

In daily life, people usually learn together. Learning can be facilitated in certain social contexts. For example, according to the social learning theory proposed by Albert Bandura,[1] individuals can observe others' behaviors and learn from the feedback given to them. In addition, one's high motivation for performing better in front of others will also facilitate learning, which is referred to as social facilitation.[2–6] It has been revealed that social cognition related areas, including dorsolateral prefrontal cortex (dlPFC), ventromedial prefrontal cortex (vmPFC), and anterior cingulate cortex (ACC), play an important role in social facilitation to learning.[4,7–9] For instance, dlPFC has been suggested to be engaged in monitoring social partners' performance and integrating this information with one's subjective goal during social learning. However, previous studies mainly focused on social facilitation to high-level learning processes such as value-based learning. To the best of our knowledge, whether and how social context can even affect low-level learning processes such as perceptual learning has not been studied yet.

Visual perceptual learning (VPL) is defined as a long-term improvement in visual task performance after training.[10–12] VPL is a commonly used paradigm for studying neural plasticity in human adults and is also an effective rehabilitation therapy for visual impairment, such as amblyopia,[13] macular degeneration,[14] and cortical blindness.[15] Many studies attempted to uncover the neural mechanisms of VPL. Electrophysiological and brain imaging studies showed that VPL could modulate neural responses in visual areas that are functionally specialized for the trained stimuli,[16–22] resulting in greater response amplitude,[18,23] shorter response latency,[24,25] sharpened tuning function,[16,20,26] stronger external noise filtering, and internal noise suppression.[19,27–29] Recent studies also suggest that VPL could be mediated by higher cortical areas, which is directly involved in decision-making processes, such as the lateral intraparietal sulcus,[30,31] ACC,[32] and dlPFC. Reweighted or optimized connections between these decision-making areas and visual areas were found to be associated with better visual task performance after training.[31,33] However, whether social cognition related areas can be engaged in VPL if subjects are trained in a social context still remains unknown.

To address the questions, we developed a novel dyadic VPL paradigm, where paired partners are trained together on a basic visual task—an orientation discrimination task, and monitor each other's performance. By combining psychophysics and functional magnetic resonance imaging (fMRI), we investigated whether the presence of a learning partner can facilitate VPL, including the behavioral performance improvement and the learning rate, as well as the differences in neural mechanisms between the dyadic and single VPL. In experiment 1, psychophysical results showed that training with a partner led to greater behavioral performance improvement and a faster learning rate than training singly. In experiment 2, we found that one's learning could be promoted even more when his/her learning partner performed better. In experiment 3, fMRI results demonstrate that, compared with the single VPL, the dyadic VPL was more effective in refining the orientation representation in early visual cortex (EVC). Interestingly, higher

The orientation discrimination thresholds in the pre-training test were submitted to a 2 × 2 mixed-design ANOVA with a between-subject factor of group (single and dyadic) and a within-subject factor of orientation (trained and untrained). The main effects of orientation ($F(1,43) = 1.439$, $p = 0.237$, $\eta^2 = 0.032$) and group ($F(1,43) = 0.034$, $p = 0.856$, $\eta^2 = 0.001$) were not significant, and the interaction between group and orientation ($F(1,43) = 0.056$, $p = 0.814$, $\eta^2 = 0.001$) was not significant either, demonstrating that the initial performances of the single and dyadic training groups were comparable.

Figure 2A shows the learning curves of the single and dyadic training groups. During the training phase, the dyadic training group exhibited better task performance and a faster learning rate, compared with the single training group. The discrimination thresholds in the dyadic training group were significantly lower than those in the single training group. This performance superiority lasted from the first to the last training sessions (all six $t(43) > 1.69$, $p < 0.05$, Cohen's $d > 0.47$, one-tailed). Both the learning curves did not saturate before the third training session. In the early training phase, the learning curve of the dyadic training group was steeper than that of the single training group. We conducted a 2 × 3 mixed-design ANOVA on the discrimination thresholds from the pre-training test and the first two training sessions, with group (single and dyadic) as the between-subject factor and day (pre-training test and training sessions 1–2) as the within-subject factor. The interaction between group and day was significant ($F(2,86) = 3.717$, $p = 0.028$, $\eta^2 = 0.080$), suggesting that the dyadic training group learned faster than the single training group in the early training phase.

Since the progress of the discrimination thresholds in the early training phase was close to linear, the discrimination thresholds in the pre-training test and first two training sessions were regressed linearly against the day. The slope of the regression line was used to quantify the learning rate. A bootstrap resampling method was used to estimate the statistical characteristics performance can help the participant to improve more in the dyadic VPL.

To further evaluate the relationship between the dyadic training effects and the performance difference between paired participants, in experiment 2, we sought to study the dyadic VPL of participants of interest who were paired with a high- or low-aptitude partner. Specifically, participants of interest (n = 30) underwent the same training as that in experiment 1. Half of the participants of interest were paired with a partner who underwent extra single training (4 daily sessions) before the dyadic training (dyadic VPL group with a high-aptitude partner, the high-aptitude group). The other half were paired with a partner who was presented with the grating stimuli embedded in white noise (dyadic VPL group with a low-aptitude partner, the low-aptitude group). These manipulations rendered the high- and low-aptitude partners perform better or worse than those participants of interest, respectively. It should be noted that, in both groups, all participants of interest and their partners did not know these manipulations. Participants of interest believed that his/her partner underwent the same training protocol as he/she did and his/her partner's performance was due to his/her own aptitude.

Before analyzing the learning data, we first examined the validity of our manipulations. For the high-aptitude partners, 4-day single training significantly lowered their orientation discrimination thresholds ($t(28) = -7.88$, $p < 0.001$, $d = 2.88$). During the following dyadic training, the average advantage index of the high-aptitude partners was 4.67 (SD = 1.88), showing that they had better task performance on most of the training days. For the low-aptitude partners, adding noise effectively elevated their discrimination thresholds and helped simulate a partner of low aptitude. The low-aptitude partners' thresholds estimated in the first dyadic training session were significantly higher than their ($t(14) = 3.49$, $p = 0.02$, $d = 0.90$) and their partner's thresholds ($t(28) = 3.10$, $p = 0.004$, $d = 1.13$) in the pre-training test. The advantage index of the low-aptitude partners was 0 for all pairs. Clearly, these results confirmed the validity of our manipulations.

Then, we analyzed the behavioral data of the participants of interest in the high- and low-aptitude groups. Figure 2A shows the learning curves of the two groups, as well as the learning curves of the single training group and the dyadic training group in experiment 1. In the pre-training test, thresholds did not differ significantly between the high- and low-aptitude groups ($F(1,28) = 0.157$, $p = 0.695$, $\eta^2 = 0.005$). In the early training phase, the slopes of the high- and low-aptitude groups were also estimated as in experiment 1, which were both steeper than that of the single training group (jackknife permutation tests, both $p < 0.001$), indicating initial faster learning rates of the dyadic training groups regardless partners' performance. Compared with the slope of the dyadic training group, the slopes of the high- and low-aptitude groups were significantly steeper and flatter, respectively (jackknife permutation tests, both $p < 0.001$), demonstrating the fastest learning rate of the high-aptitude group. As the training proceeded, the high-aptitude group rather than the low-aptitude group, showed superiority over the single training group. In the post-training test, the performance improvement of the high-aptitude group was significantly greater than that of the low-aptitude group ($t(28) = 1.845$, $p = 0.038$, $d = 0.67$, one-tailed; Figure 2B). But there was no significant difference between the single training group and the low-aptitude group ($t(28) = -0.56$, $p = 0.583$, $d = 0.20$) as well as between the dyadic training and the high-aptitude group ($t(43) = -0.06$, $p = 0.95$, $d = 0.02$). Taken together, these results demonstrate that one's learning rate and performance improvement can be impacted by his/her learning partner's performance.

Neural substrates of enhanced learning effects in dyadic VPL

In experiment 3, another 30 participants were recruited to investigate the neural substrates of the enhanced learning effects in the dyadic VPL. We sought to address two questions. One was the neural underpinnings of the enhanced performance improvement of the dyadic VPL in the post-training test, the other was the differences in neural activity and functional connectivity between the dyadic and single VPL during training.

To this end, participants were randomly split into two groups: the single training group (n = 10) and the dyadic training group (n = 20, 10 pairs of participants). All participants underwent three phases: pre-training test, training, and post-training test. During each test phase, a psychophysical test was first conducted to measure the orientation discrimination thresholds at 0°, 45°, and 90° deviated from the trained orientation all either clockwise or counterclockwise (hereafter referred to as 0°, 45°, and 90°). The psychophysical test was identical to that in experiment 1. 1 day after the psychophysical test, all participants in the single training group and one of each pair of participants in the dyadic training group (10 participants in each group) underwent an fMRI test (Figure 3C). They were asked to perform the orientation discrimination task at 0°, 45°, and 90° during scanning, so we could investigate how training affected the orientation representations in the brain.

The training phase consisted of five daily training sessions. For the dyadic training group, paired participants finished 5 single training runs and 5 dyadic training runs in the first daily training session, so we could make a within-subject comparison and identify the neural activity differences between the two kinds of training. In the dyadic training runs, participants of interest were scanned when they practiced the training task. His/her partner practiced this task together, but outside the scanner (Figure 3A). In the single training runs, participants of interest were scanned when they practiced the training task singly. Except the first training session, the other 4 training sessions were completed in a behavioral room. Paired participants received the dyadic training similar to that in experiment 1. For the single training group, participants completed 10 single training runs in the scanner in the first daily session, and in the other 4 training sessions, they received the single training identical to that in experiment 1 in a behavioral room.

To better compare the single training and the dyadic training, in this experiment, we simplified the dyadic VPL paradigm in experiment 1. We removed the second response and gave paired participants the final feedback after their first and independent responses. They could still know each other's performance through the feedback (Figure 3B). We found that this simplified paradigm replicated the learning facilitation effects in experiment 1. Participants in the dyadic training group exhibited a faster learning rate (jackknife permutation test, $p < 0.01$) and greater performance improvement in the post-training test compared with those who received single training ($t(18) = 2.75$, $p = 0.01$, $d = 1.23$; Figure 4E).

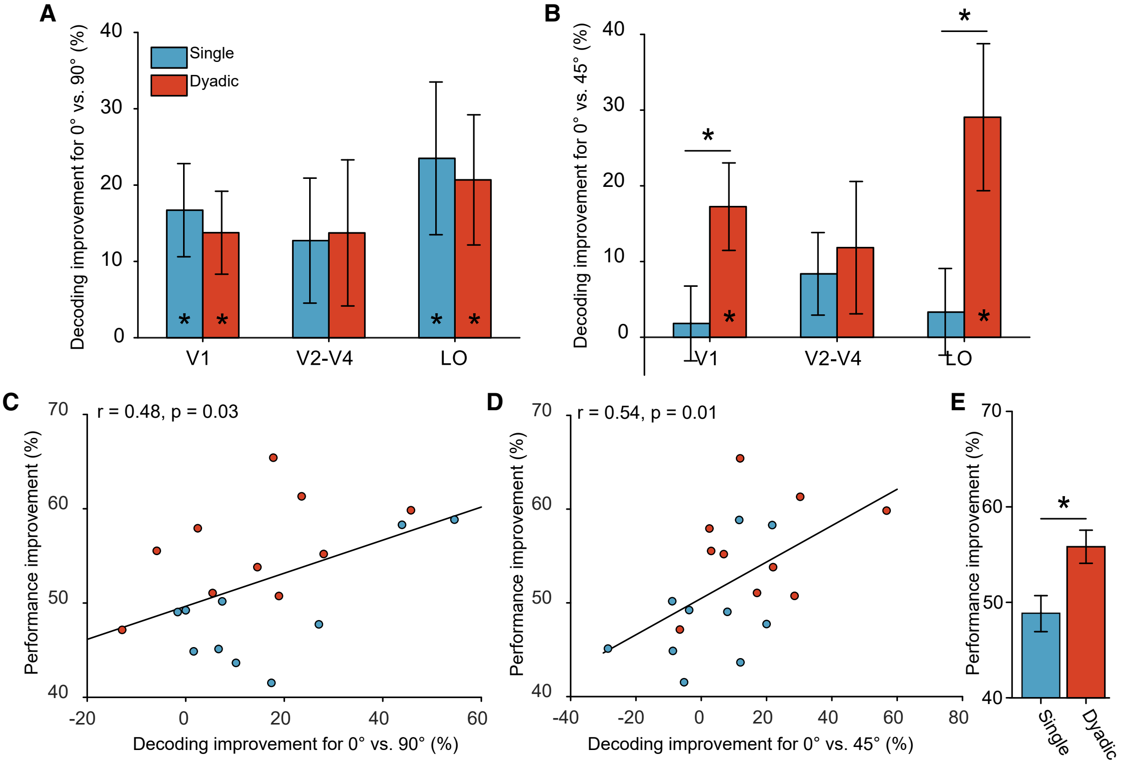


Figure 4. Results of experiment 3

(A and B) Performance improvements for decoding 0° versus 90° (A) and 0° versus 45° (B) in visual areas (*$p < 0.05$).

(C and D) Correlations between behavioral performance improvement and decoding performance improvement in V1 for 0° versus 90° (C) and 0° versus 45° (D).

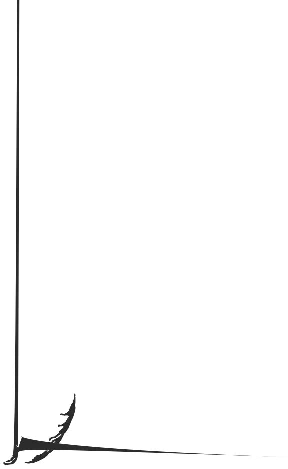
(E) Behavioral performance improvements after the dyadic and single training (*$p < 0.05$). Error bars denote 1 SEM across participants.

paired participants underwent the orientation discrimination training, during which one could monitor his/her partner's performance at the end of each trial via connected computers. Using this paradigm, in experiment 1, we found that learning with a partner could significantly facilitate VPL, resulting in a greater behavioral performance improvement and a faster learning rate. In experiment 2, we found that the performance difference between paired partners could modulate the behavioral performance improvement. In experiment 3, the fMRI results demonstrate that, relative to the single VPL, the dyadic VPL gave rise to more refined orientation representations in V1 and LO. Such refinements might be due to the interplay between early visual areas and higher areas including IPL and dlPFC, in which different activation patterns and functional connectivities to EVC were observed during the single and the dyadic training.

It might be argued that the greater behavioral performance improvement and the faster learning rate could be simply due to more behavioral responses, rehearsal time, and feedbacks in the dyadic VPL, rather than the social context. The results obtained from experiments 2 and 3, however, argue against this explanation. It can be seen in experiment 2 that the performance of participants paired with a low-aptitude partner did not exhibit the VPL facilitations although they made a second response, had more rehearsal time, and received a second feedback. In experiment 3, participants in the dyadic training group still exhibited similar VPL facilitations to those in experiment 1, even though the second response and feedback were removed, which made the numbers of feedback and response equal between the single and the dyadic VPL groups.

It might also be argued that attention or vigilance level could explain the behavioral learning effects. We believe this explanation is unlikely. First, the univariate fMRI data analysis did not reveal any significant difference between the dyadic and the single training. If the attention explanation were right, we should have observed stronger BOLD signals in visual cortex and the fronto-parietal attention network during the dyadic training, relative to the single training. However, this is not the case. Second, in both the pre- and post-training tests for the single training and the dyadic training groups, subjects performed the orientation discrimination task equally well (75% correct) in the scanner, demonstrating that there is no difference in task difficulty and, presumably, attention. However, note the decoding accuracies in V1 and LO increased more after the dyadic training, relative to the single training.

In the dyadic VPL, the presence of a learning partner creates a context for social facilitation,[38,39] which may account for the behavioral learning effects, as one of possible explanations. First, compared with performing the training task singly, individuals have a higher motivation and increased alertness to perform better when in front of a learning partner, a phenomenon known as social facilitation, or audience effect.[40] Second, when inconsistent responses occur, one would gradually become aware of



the performance difference between him/her and his/her partner throughout the training process, which would lead to social comparison. Learning with a high-aptitude partner could result in more feelings like “my partner is correct, and I am wrong,” which would threat one’s self-esteem. Such an upward comparison might give rise to higher motivation that could stimulate the participants to concentrate and improve their performance more.[41,42] On the other hand, the downward comparison when learning with a low-aptitude partner might protect one’s self-esteem and attenuate the social facilitating effect, thus leading to a comparable improvement to the single training.[43]

Converging evidence shows that motivation and social comparison are associated with several key brain areas, including dlPFC, IPL, vmPFC, dorsal ACC, and striatum.[38,44] Especially, dlPFC has been considered as a pivotal hub to integrate information from different sources,[45] make strategic responses[46,47] and motivate behaviors.[7,8] For instance, McDonald et al. found that with the single training, the dyadic training was more effective in refining the orientation representations in V1 and LO, which contributed to the greater behavioral performance improvement. These results suggest that high-level social cognition processes such as social facilitation could even impinge EVC and shape the characteristics of its neural responses. Our study is reminiscent of previous findings that other high-level cognitive processes, such as reinforcement, could influence neural activity in EVC. Behavioral studies from Seitz et al.[52] and Wang et al.[53] have consistently found that reward-evoked VPL does not transfer from the trained eye to the untrained eye, indicating a change at an early stage of the visual processing hierarchy. Arsenault et al.'s neuroimaging study also found that the dopaminergic reward signal selectively shapes neural activity in the EVC.[54]

Finding new ways to augment brain functions effectively and rapidly is a perennial issue in medical and neuroscience communities.[55] In the past decades, numerous studies have shown that VPL can reliably enhance long-term visual abilities and have irreplaceable advantages in treating neuro-ophthalmic disorders.[10,13,15,56] To achieve greater effectiveness and better clinical applications, several add-on methods combined with visual training have been proposed to enhance VPL, including transcranial electricity stimulation (tES) and adjunctive medications. Yang et al.[57] found that transcranial direct current stimulation (tDCS) over visual cortex could improve behavioral performance by facilitating awake consolidation of VPL. He et al. found that 10 Hz transcranial alternating current stimulation (tACS)[58] over visual cortex could help subjects acquire greater performance improvement within a shorter time. Rokem and Silver[35] reported that the cholinesterase inhibitor donepezil could also significantly augment the magnitude of VPL. The current study introduces a new VPL paradigm and demonstrates that learning with a partner can increase the magnitude of performance improvement and accelerate the learning rate. Compared with tES and medications, this paradigm is more tolerable, less costly, and bears minimal risk of side effects, providing a possible way to treat visual and ophthalmic disorders more effectively and rapidly.

In conclusion, we found that the social facilitation resulted from learning together could remarkably boost the low-level VPL, significantly modify the activity patterns in bilateral parietal cortex and left dlPFC and enhance their connectivities with EVC, and profoundly refine the orientation representations in visual cortex. These findings also provide new insights for potential clinical interventions and enhancements on visual and even broader cognitive functions.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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ACKNOWLEDGMENTS

We thank Dr. Qian Wang, Dr. Xiaoqing Wang, and Dr. Tao He for their helpful comments on the draft. This work was supported by the National Science and Technology Innovation 2030 Major Program (2022ZD0204802), the National Natural Science Foundation of China (31930053), and Beijing Academy of Artificial Intelligence (BAAI).

AUTHOR CONTRIBUTIONS

Y.Z., J.L., Y.W., and F.F. designed research. Y.Z., K.B., and F.F. performed research. Y.Z., K.B., and F.F. analyzed data. Y.Z., J.L., and F.F. wrote the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

Received: July 4, 2022
Revised: February 24, 2023
Accepted: April 26, 2023
Published: May 23, 2023

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Human behavioral and fMRI data	This paper	https://osf.io/yka9v/
Software and algorithms		
MATLAB R2019a	The MathWorks, Natick, Massachusetts, USA	https://www.mathworks.com/
Psychtoolbox 3.0.13	Brainard[59]	https://www.psychtoolbox.org/
SPM12	Penny et al.[60]	https://www.fil.ion.ucl.ac.uk/spm/software/spm12/
The decoding toolbox 3.997	Hebart et al.[61]	https://www.bccn-berlin.de/tdt
BrainVoyager QX 2.4	Brain Innovations, Maastricht, the Netherlands	https://www.brainvoyager.com/
Custom MATLAB scripts for analysis and statistical tests	This paper	Code is available via open science framework: https://osf.io/yka9v/
Other		
3T Siemens Prisma MRI scanner	Center for MRI Research at Peking University	http://www.aais.pku.edu.cn/yjzx/
64-channel phase-array head coil	Center for MRI Research at Peking University	http://www.aais.pku.edu.cn/yjzx/

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources should be directed to and will be fulfilled by the lead contact, Fang Fang (ffang@pku.edu.cn).

Materials availability

This study did not generate new reagents.

Data and code availability

- All human behavioral and fMRI data are available for download on open science framework (https://osf.io/yka9v/).
- Custom MATLAB scripts for analysis and statistical tests is available via open science framework: https://osf.io/yka9v/
- Any additional information required to re-analyze the data reported in this paper is available from the lead contact upon request

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Human participants

There were 45 participants (20 males) in Experiment 1, 60 participants (23 males) in Experiment 2, and 30 participants (15 males) in Experiment 3. All participants were right-handed with reported normal or corrected-to-normal vision and had no known neurological or visual disorders. They were naïve to the purpose and design of this study. Their ages ranged from 18 to 27 years. They gave written, informed consent in accordance with the procedures and protocols approved by the human subject review committee of Peking University.

METHOD DETAILS

Behavioral and imaging data acquisition

In the psychophysical experiments, visual stimuli were presented on a Display++ 32-inch monitor (Cambridge Research Systems Ltd; refresh rate: 100Hz; spatial resolution: 1024×768) with a gray background (30 cd/m^2) at a viewing distance of 70 cm. A head and chin rest were used to stabilize participants' head position.

The fMRI experiments were performed on a 3T Siemens Prisma MRI scanner at the Center for MRI Research at Peking University. MRI data were acquired with a 64-channel phase-array head coil. In the scanner, visual stimuli were back-projected via a video projector (refresh rate: 60 Hz; spatial resolution: 1024×768) onto a translucent screen placed inside the scanner bore. Participants viewed the stimuli through a mirror mounted on the head coil. The viewing distance was 70cm. Blood-oxygen-level-dependent (BOLD) signals were measured using an echo-planner imaging (EPI) sequence with a multiband acceleration factor of 2 (TE: 30ms; TR: 2000ms; flip angle: 90°; acquisition matrix size: 112×112; FOV: 224×224 mm^2; slice thickness: 2mm; number of slices: 62; slice orientation: transversal). FMRI slices covered the whole brain. In each MRI session, a T1-weighted high-resolution 3D structural dataset were acquired for each participant before functional runs using a 3D-MPRAGE sequence (voxel size: 1×1×1mm^3).

Stimuli and design

Visual stimuli were ring-shaped sinusoidal gratings with their edge smoothed with a Gaussian filter (outer radius: 4°; inner radius: 1°; Michelson contrast: 1.0; spatial frequency: 2 cycles/°; mean luminance: 30 cd/m^2). The phase of the gratings was randomized. The spatial frequency also changed slightly in each grating, which was randomly drawn from a Gaussian distribution with a mean of 2 cycles/° and a standard deviation of 0.02 cycles/°. In the dyadic training sessions in Experiment 2, the gratings presented to the 'low-aptitude' partner were embedded in white noise. The root-mean-square (RMS) contrast of the noise was 0.72. The RMS contrast is defined as the standard deviation of pixel luminance values divided by the mean pixel luminance.[62,63]

Experiment 1

In Experiment 1, we investigated how dyadic training affected the learning rate and performance improvement compared with the single training. Participants were randomly assigned into the single training group (n=15) or the dyadic training group (n=30), in which they were trained on an orientation discrimination task singly or in pairs. Both groups underwent three phases:iew.9(groups)-185.Iradi98.8qyadin si7

Experiment 3

In Experiment 3, we investigated the neural substrates of the enhanced learning effect in the dyadic VPL. Similar to Experiments 1 and 2, Experiment 3 also consisted of three phases: pre-training test, orientation discrimination training, and post-training test. During each test phase, we first measured the orientation discrimination thresholds at 0°, 45°, and 90° deviated from the trained orientation all either clockwise or counter-clockwise (hereafter referred to as 0°, 45°, and 90°), using the method of constant stimuli in Experiment 1. One day after acquiring the thresholds, we measured BOLD signals responding to the three orientations (i.e., 0°, 45°, and 90°) in 8 fMRI runs. Each run contained 12 stimulus blocks of 12s, four blocks for each of the three orientations. Stimulus blocks were interleaved with blank blocks of 12s. Each stimulus block consisted of six trials. In a trial, two gratings were each presented for 100 ms. They were separated by a 500 ms blank interval and were followed by an 800 ms blank interval. Participants were asked to make a 2-AFC judgement of the second orientation relative to the first one by pressing one of two buttons. The next trial began 500ms after button press. Here, the orientation change between the two gratings was the discrimination threshold measured in the psychophysical test and made participants perform equally well (75% correct) across the three orientations.

The training phase consisted of 5 daily sessions. For the dyadic training group (n=20), in the first session, all participants completed 5 single training runs and 5 dyadic training runs, but only the participants of interest were scanned. In both kinds of training runs, there were 12 stimulus blocks of 12 s, interleaved with 12 blank blocks of 12 s. The trial structure was similar to that in the fMRI test except that informative feedback was provided for 1 s after response, making each block contain only 4 trials instead of 6 trials. In the single training runs, participants completed the task singly, and feedback was provided by changing the color of the fixation to green (correct response) or red (wrong response). In the dyadic training runs, only the participant of interest was in the scanner. His/her partner completed the task together, but outside the scanner. Feedback was provided by changing the color of the fixation to green (both correct), red (both wrong), blue (correct and inconsistent with partner), or yellow (wrong and inconsistent with partner). Participants were instructed on the meaning of the feedback before scanning. At the beginning of each run, participants were informed that this run was a single or dyadic training run. In the rest 4 training sessions, paired participants underwent the dyadic training in the behavioral room. The dyadic training was similar to that in Experiment 1, except the second response part was removed. After paired participants made their first independent responses, they received the final feedback immediately. The feedback was both correct, both wrong, or which participant was correct.

For the single training group (n=10), during the first training session, participants completed 10 single training runs in the scanner. In the rest 4 training sessions, they underwent the single training in the behavioral room. The single training was identical to that in Experiment 1.

In the retinotopic mapping session, we defined retinotopic visual areas (V1, V2, V3, V4, and LO) using a standard phase-encoded method developed by Sereno et al.,[35] Engel et al.,[36] and Wandell et al.[37] in which participants viewed a rotating wedge that created traveling waves of neural activity in visual cortex. We also performed a localizer run to identify voxels in the retinotopic areas responding to the trained stimuli. This block-design localizer run contained 12 stimulus blocks of 12 s, interleaved with blank blocks of 12 s. A full contrast checkerboard stimulus flickering at 7.5Hz was presented in stimulus blocks. The size and the location of the checkerboard stimulus were identical to those of the trained ring-shaped gratings.

QUANTIFICATION AND STATISTICAL ANALYSIS

Behavioral data analysis

Behavioral data were processed using MATLAB (MathWorks), Psychtoolbox,[59] and custom scripts. To estimate the orientation discrimination thresholds, the percentage of trials in which participants made a correct response was plotted as a psychometric function of the orientation change. We used a Weibull function to fit the psychometric values and interpolated the data to find the 75% accuracy point (i.e., the orientation discrimination threshold). The behavioral performance improvement was calculated as

$$\left(threshold_{pre-training\ test} - threshold_{post-training\ test}\right) / threshold_{pre-training\ test} \times 100\%$$

To characterize the learning process, thresholds of the pre-training test and training sessions 1-3 were regressed linearly against the day. The slope was used to quantify the learning rate. Since the data did not allow a reliable slope estimation at the single participant level, bootstrap and non-parametric permutation methods were used to examine the slope difference between groups. A bootstrap method was used to estimate the mean, variance, and confidence interval of the slope.[64] In each bootstrap sampling, we randomly sampled *n* participants with replacement (*n* was the group size), and then estimated the thresholds. After averaging the thresholds of the n sampled participants, the linear regression was performed to estimate the slope. The slope distribution was estimated by bootstrap sampling 5,000 times for each group. In the permutation test, a jackknife procedure was employed.[34] The model was fit to *n* resamples from the data. For each resample, the data from one participant were omitted, and the thresholds from the remaining *n*-1 participants were averaged. The slope was then estimated for the averaged thresholds. This produced *n* different values of slope and built a jackknife sample. The values of slope were then compared across the jackknife samples. 10,000 permuted samples were created by randomly recoding the group from which each slope was taken. The actual difference between the means

fMRI data analysis

fMRI data were processed using BrainVoyager QX (Brain Innovations, Maastricht, the Netherlands), MATLAB (MathWorks), SPM12,[60] the decoding toolbox,[61] and custom scripts. The anatomical volume in the retinotopic mapping session was transformed into the AC-PC space and then inflated using BrainVoyager QX. Functional volumes in all sessions were preprocessed, including 3D motion correction, linear trend removal, and high-pass filtering (cut-off frequency: 0.015 Hz) using BrainVoyager QX. The functional volumes were then aligned to the anatomical volume in the retinotopic mapping session and transformed into the AC-PC space. The first 6 s of BOLD volumes were discarded to minimize transient magnetic saturation effects. A general linear model (GLM) procedure was used to define the ROIs. The ROIs in V1-V4 and LO were identified as a set of contiguous voxels that responded more strongly to the checkerboard stimulus than the blank screen ($p<0.05$, FDR corrected) in the localizer run.

With the fMRI data in the pre- and post-training tests, decoding analysis was performed to classify the activation patterns evoked by two orientations. A GLM procedure was first used to estimate beta values for individually responsive voxels in each stimulus block. The 100 most responsive voxels of each ROI were chosen to conduct the decoding analysis. The beta values of these voxels were then normalized in each run, resulting in 32 patterns (corresponded to 32 stimulus blocks) per test for each orientation. These patterns were used to train linear support vector machine (SVM) classifiers. A leave-one-run-out cross-validation procedure was used to calculate the decoding accuracy. Specifically, 28 patterns from 7 of 8 runs were chosen to train the classifier, and the remaining 4 patterns from the test run were used to estimate the decoding accuracy. The decoding improvement was calculated as $(Acc_{post-training\ test} - Acc_{pre-training\ test})/Acc_{pre-training\ test} \times 100\%$, where Acc stands for decoding accuracy.

FMRI data in the first training session of the dyadic training group was first analyzed using a univariate method to examine whether there was any difference in overall BOLD activity between the single and dyadic training runs. The individual preprocessed functional imaging data was normalized to the template brain, smoothed using a 3D-Gaussian kernel of 6 mm FWHM, and then submitted to a GLM contained 2 regressors for the training types (single or dyadic) and 9 nuisance regressors accounting for run effects. Linear contrasts of estimated voxel-wise parameters were computed at the individual level and then taken to group-level t tests. Significance of the test was determined at either FWE $p<0.05$ or uncorrected $p < 0.001$, cluster size $k > 50$.

A searchlight analysis was then implemented to uncover any potential difference in neural activation pattern between the single and dyadic training runs. FMRI data during the single and dyadic training were firstly normalized to the template brain. Then we performed a volume-based searchlight analysis by sliding a 4-voxel-radius spherical linear SVM classifier voxel-by-voxel over the whole brain. The activity patterns within each searchlight were used to decode the training type by using a leave-one-run-out cross-validation procedure. To identify brain regions where the decoding accuracy was significantly higher than chance level, we performed second-level analyses by using voxel-wise one-sample t-tests on smoothed accuracy maps with a 3-D Gaussian kernel of 4 mm FWHM. This generated a voxel-wise whole-brain t-map reflecting the statistical significance of the decoding accuracy. Significance of the test was determined at uncorrected $p < 1\times10^{-5}$, cluster size $k > 50$.

Furthermore, we conducted PPI analysis to uncover how the functional connectivity between a given ROI (seed region) and a target region is modulated by a psychological variable. A 3D-Gaussian kernel of 6 mm FWHM was firstly used to smooth the EPI images. The seed brain regions were determined based on the searchlight analysis above. We used as a seed the average BOLD time series